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A fern-bennettitalean floral assemblage in Tithonian-Berriasian travertine deposits (Aguilar Formation, Burgos-Palencia, N Spain) and its palaeoclimatic and vegetational implications

Una asociación florística de helechos-bennettitales en acumulaciones travertínicas del Titónico-Berriasiense (Formación Aguilar, Burgos-Palencia, España) y sus implicaciones paleoclimáticas y vegetacionales

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Abstract

This report describes a macrofloral fossil assemblage discovered in travertine deposits of the Tithonian-Berriasian Aguilar Formation (provinces of Palencia and Burgos, N Spain). The assemblage includes megaremains of a single species of Filicales (Cladophlebis denticulata) and of eleven taxa tentatively identified as Bennettitales (Otozamites mundae, Otozamites sp., Ptilophyllum pecten, Ptilophyllum pectiniformis, Ptilophyllum sp. cf. pectiniformis, Ptilophyllum acutifolium, Ptilophyllum sp., Pterophyllum cycadites, Pterophyllum sp. cf. thomasii, Zamites pumilio, and cf. Pseudocycas sp.). Specimens were preserved as impressions coated with a microbial film up to 5 mm thick made up of: bacteria and cyanobacteria. Based on the available sedimentological and palaeobotanical data, a dry-savannah vegetation and an arid climate were deduced. Late Jurassic macrofloras are globally scarce and have not previously been reported in Spain. Hence, the Aguilar Formation macroflora provides valuable information on the coeval phytogeography and palaeoclimate of southwestern Europe. Furthermore, the lack of floras observed so far in palaeotravertine deposits older than Pliocene in age makes this macroflora exceptional.

Keywords: Filicales, Bennettitales, Palaeotravertine, Tithonian, Berriasian, Biofilms.

Resumen

Se describe por vez primera vez una macroflora fósil acumulada en facies travertínicas de edad Titónico-Berriasiense, correspondientes a la Formación Aguilar (provincias de Burgos y Palencia). Esta macroflora incluye una especie de Filicales (Cladophlebis denticulata) y once taxa atribuibles al Orden Bennettitales (Otozamites mundae, Otozamites sp., Ptilophyllum pecten, Ptilophyllum pectiniformis, Ptilophyllum sp. cf. pectiniformis, Ptilophyllum acutifolium, Ptilophyllum spp., Pterophyllum cycadites, Pterophyllum sp. cf. thomasi, Zamites pumilio, and cf. Pseudocycas sp.). Los ejemplares corresponden a impresiones de restos de hojas cubiertos por un velo microbiano bien preservado, de cerca de 5 mm, formado por bacterias y cianobacterias. La composición de la flora y los datos sedimentológicos permiten inferir una vegetación de sabana que se desarrollo bajo un clima árido.

Las macrofloras del Jurásico Superior son escasas a escala mundial, no habiendo sido descrita ninguna en España. Por todo ello, la macroflora de la Formación Aguilar aporta una relevante información que puede contribuir a una mejor comprensión fitogeográfica y paleoclimática del suroeste de Europa en dicha edad. Además, la ausencia, a nivel global, de floras acumuladas en travertinos anteriores al Plioceno, permite considerar esta macroflora como excepcional.

Palabras clave: Filicales, Bennettitales, Paleotravertino, Titónico, Berriasiense, Velos microbianos.

1. Introduction

Late Jurassic and/or Early Cretaceous macrofloras are relatively scarce in Western Europe. Despite this, there are documented macrofloras for the Late Jurassic (Portlandian) of: Germany (Sternberg,1823,1838; Salfed, 1907; Berry, 1918; Mutschler, 1927; Krausel, 1943; Meyer, 1974); Scotland (Seward, 1911; Van der Burgh, and van Konijnenburg- van Cittert, 1984; van Konijnenburg-van Cittert and van der Burgh, 1989; Thomas and Batten, 2001; van Koninjnenburg- van Cittert, 2008); South of England (Buckland, 1828; Fitton, 1836; Carruthers, 1870; Seward, 1897; Francis, 1983; 1984; Cleal *et al.*, 2001; van Koninjnenburg-van Cittert, 2008); France (Saporta, 1873, 1894; Ginsburg, 1973; Barale, 1978, 1981; Roman *et al.*, 1994); and Portugal (Heer, 1881; Saporta, 1894; Teixeira, 1948; Pais, 1974, 1998). In Spain, the only description so far is that of a Kimmeridgian conifer specimen from Barcelona province (*Pagiophyllum cirinicum* (Saporta); Barale and Calzada, 1985). The macroforal assemblage described here is ascribed to the Tithonian-Berriasian (see below).

This floral assemblage was discovered a decade ago close to the Villela Fault at the southern margin of the alluvial-palustrine Aguilar Basin (Hernández, 2000). The assemblage was detected in channel-shaped rock bodies intercalated within palustrine limestones that were interpreted by Hernández *et al.* (1998) as fossil travertines (carbonate deposits precipitated in hot springs). The significance of this finding is that, compared to the extensive outcrops of Quaternary and Pliocene travertines, pre-Tertiary travertines are scarce. The presence of plant remains in travertines is also extremely rare. In their initial report, Hernández *et al.* (1998) provided a list of the plant species encountered but did not describe them. Here, we document and describe in detail the composition of this floral assemblage and discuss its palaeoecological and palaeoclimatic significance.

2. Material and methods

A total of 74 identifiable plant remains were collected with a distribution as follows: ferns (8.2 per cent) and bennettitaleans (91.8 per cent). All specimens are preserved as calcite-filled impressions (part and counterpart in many cases) lacking cuticles. Most specimens were heavily encrusted within the travertine, which, in large measure, hindered observation of foliar venation.

Owing to the state of preservation of the specimens, the cuticle analyses necessary for the accurate identification of plant remains could not be conducted. Furthermore, with the exception of the fern specimens, the lack of cuticles means that the flora here described can only tentatively be ascribed to the Order Bennettitales, as recommended by Rees and Cleal (2004) in their study of specimens in a similar state of preservation from Antarctica.

We could thus only apply morphometric methods and techniques in our analysis of the specimens found. For the identification of bennettitalean material we adopted the criteria described by Harris (1969) and modified by Watson and Sincock (1992). The diagnostic characters selected were: (1) rachis and leaflet dimensions and ornamentation; (2) basal leaflet shape; (3) leaflet insertion angle; (4) leaflet outline; (5) leaflet width:length ratio; and (6) leaflet arrangement.

Specimens were observed under a Zeiss Stemi 1000 binocular microscope. For observations at higher magnification and measurements, a Leica MZ 16 A binocular microscope was used. Photographs were taken with a Canon Eos 3000 Digital camera.

3. Geological setting

The Aguilar Formation comprises a thick succession (up to 600 m) of alluvial and palustrine deposits that infilled an ancient fault-bounded basin (Hernández *et al.*, 1995; Pujalte *et al.*, 1996) in the southwest Basque-Can-

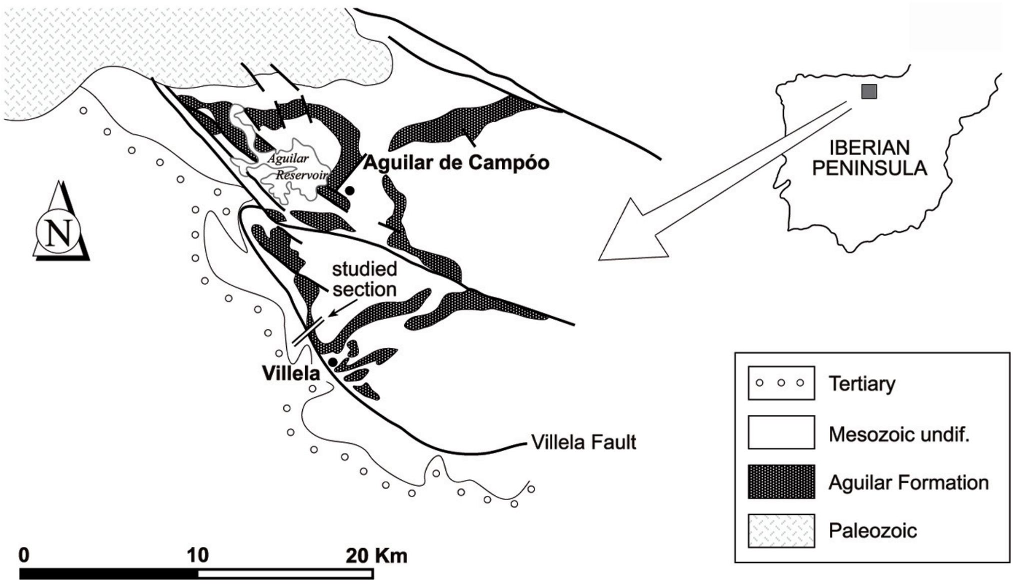

Fig. 1. - Geological map of the Aguilar Basin showing the location of the Aguilar Fm. outcrops and the studied section.
Fig. 1.- Mapa geológico de la Cuenca de Aguilar mostrando los afloramientos de la Fm. Aguilar y la sección estudiada.

tabrian Region (Fig. 1). As a result of this tectonically active context, the unit shows great stratigraphic complexity, including a succession with vertically alternating carbonate palustrine phases and detritic alluvial episodes. This situation originated by syn-sedimentary activity of the Villela Fault, which determined the progradation of alluvial systems and the formation of carbonate wetlands (Pujalte *et al.*, 2004).

Three main carbonate members have been differentiated in the Aguilar Formation, all of which developed in palustrine settings. From bottom to top, these are the Santa María la Real Member, Prandillera Member and La Presa Member. Along the southwest border of the Aguilar Basin, these carbonate units appear intercalated with lutite and calcareous conglomerate facies with frequently reddish marine Jurassic clasts, defined as the Becerril Member.

The fossil plant remains here described and interpreted were obtained from the lower Santa María la Real Member in the Villela section, occupying the southwest Aguilar Basin (Fig. 2). In this section, the Santa Maria la Real Member comprises massive, compact, well-cemented light grey limestones, forming tabular beds 0.5-1 m thick. According to their texture, these limestones can be defined as wackstones or packstones, and they usually contain abundant charophyte remains (in life position), ostracods and freshwater gastropods. Very often, the tops of the layers present features related to subaerial exposure, such as pseudomicrokarst or rhizoliths (Hernández *et al.*, 1997). Diffuse horizontally stratified beds composed of grey marls also appear interlayer the limestones. This facies association can be interpreted as the deposition of biogenic carbonate in a low-energy, shallow, freshwater environment, probably a wetland, where exposure processes eventually took place. Finally, marl micro-horizons could indicate times of greatest clastic influx.

Vertically and laterally, the facies are gradually replaced with light grey to bright red limestones and marly limestones, displaying a variety of postdepositional textures (pedogenic modifications) such as pseudomicrokarsts, marmorization features, desiccation cracks, black pebbles, nodular horizons, breccias, circumgranular cracks, glaebulae, and both peloidal and grumelar textures. This facies association seems to reflect an intense pedogenic response to subaerial exposure of palustrine limestones during long periods of time and ephemeral humectation phases (Freytet and Plaziat, 1982; Armenteros *et al.*, 1997), both occurring in a marginal area of the wetland system.

The two facies associations described in the Santa María la Real Member, palustrine limestones and pedogenic modified limestones, appear organised in vertical sequences that indicate processes of gradual desiccation of a freshwater wetland, related to the activity of the Villela fault system. However, it is widely accepted that a change in climate towards drier conditions may also have shaped these sequences.

Exceptionally, a few channelized bodies were found interbedded between the palustrine limestones. This lithosome layer, up to 2 m thick, was topped by concentrically laminated spherical oncoid levels (delicate shrub-like layers). Biomicrite is the most characteristic lithol-

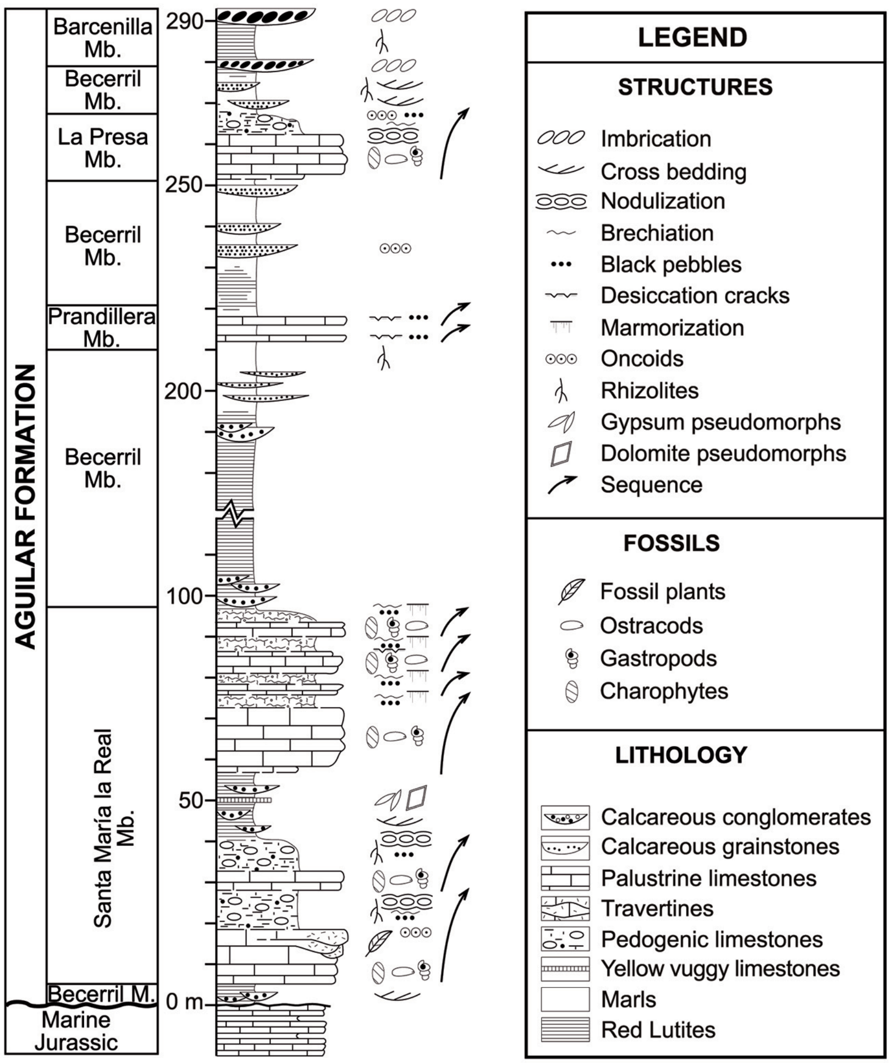

Fig. 2.- Stratigraphic section of the Aguilar Fm. near to Villela showing the location of the fossil plants.
Fig. 2.- Serie estratigráfica de la Fm. Aguilar en las proximidades de Villela, mostrando la situacion de las plantas fósiles.

ogy of this facies, showing intense and well developed bacterial and cyanobacterial laminar textures coating the plant remains (Hernández *et al.*, 1998). Bacterial growth is the most distinctive texture and appears as multiple layers of irregular morphology displaying microscopic shrub-like colonies, and filamentous and coccoid microbial mat depositions. Cyanobacterial deposits occur as bush-like or fan-like calcifications and laminar microlayers. Frequently, the filamentous colonies are tilted about 30º. This facies association can be interpreted as a travertine system, formed in a hot-spring related to a hydrothermal source and marginally connected to the main carbonate wetland. The temperature and chemistry of the hot-spring waters would not have been favourable for the growth of autochthonous vegetation in the stream, but conditions allowed for the development of bacterial and cyanobacterial communities. Finally, concentric oncoid layers when closely associated with bacterial and cyanobacterial communities indicate intermittently agitated pools.

According to the charophyte assemblage (Hernández *et al.*, 1999), the Santa María la Real Mb. belongs to the *Maillardii* biozone (Late Tithonian-Early Middle Berrisian). Further, the presence of *Clavator reidii* var. *pseudoglobatoroides* (SCHUDACK) at the top of the Santa María la Real Mb. dates the unit as Early Berrisian (Schudack, 1987). Although the age of the base of this member cannot be more precisely determined using charophyte data, the occurrence of *Cypridea* gr. *tumescens* (ANDERSON), *Leiria striata* HELMDACH and *Theriosynoecum forbesi* (JONES) ostracods (Caballero *et al.*, 1998) in the underlying Becerril Mb. confirms the Late Tithonian age of the base of the Santa María la Real Mb. (*Theriosynoecum forbesi* biozone of Horne, 1995).

In conclusion, the information that can be inferred from both the charophyte and ostracod assemblages attribute the Santa María la Real Mb. (and consequently the fossil plant remains of its travertine facies) to the Late Tithonian-Early Middle Berriasian.

4. Systematic palaeontology

Order FILICALES
Family unknown
Genus *Chladophlebis* Brongniart 1849
Cladophlebis denticulata (Bongniart) Fontaine emend. Harris, 1961
Figures 3, 4
Material. MNCNV-7990, MNCNV-7991, MNCNV-7992, MNCNV-7993, MNCNV-7994, MNCNV-7996.

Description. Small vegetative pinna fragments. Rachis flat, 0.5-0.6 mm wide, rounded basally bearing subopposite pinnules 6-7 mm long and 2.5-3 mm wide, thin, subtriangular, slightly falcate and inclined forwards, with parallel, slightly dentate margins, rounded to obtuse apex, broadly based but not confluent, contracted basally. Pinnules arise from the rachis at 66º. Pecopteroid venation, midrib straight, prominent, with seven pairs of lateral veins that bifurcate near the midvein.

Remarks. This species is rare in Villela, comprising 8.2 per cent of the remains. It occurs as impressions (part and counterpart in one case) of portions of last order pinnae. In many cases the imprints were calcite-filled.

The pinnules of the specimens recovered are smaller than those described by Harris (1961) from the Yorkshire material. Nevertheless, Harris (*op. cit.* p.86) described a specimen assigned to this species, which is deposited in the Sedgwick Museum, with exceptionally small pinnules comparable to the Villela material. *Cladophlebis denticulata* was distributed widely geographically and stratigraphically during the Jurassic and Berriasian-Barremian and commonly appears in outcrops of Europe (Seward, 1911; Gothan, 1914; Harris, 1961); America (Fontaine, 1889; Menéndez, 1951); Asia (Kawasaki, 1925; Oishi, 1932; Sze, 1949) and Oceania (Arber, 1917).

Class GNETOPSIDA
Order Bennettitales
Family Unknown
Genus *Otozamites* Braun 1843 emend. Watson and Sincock, 1992
Otozamites mundae (Morris) Teixeira, emend. Pais, 1974
Figure 5
Material. MNCNV- 7933; MNCNV- 7937; MNCNV-7941; MNCNV- 7999

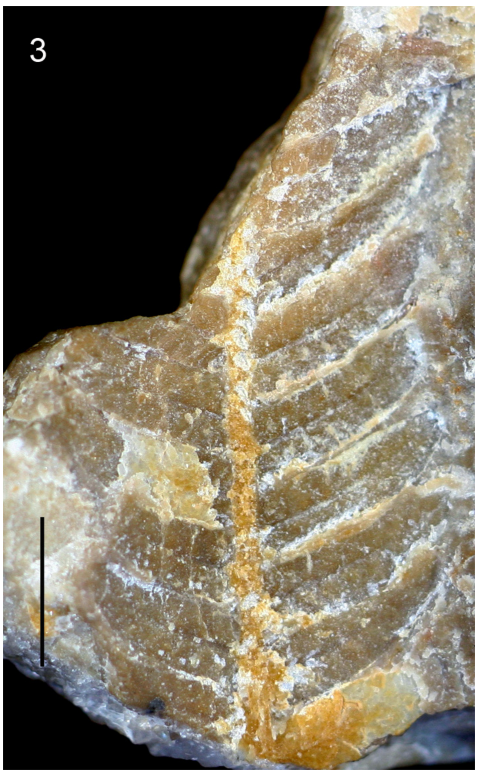

Fig. 3.- *Cladophlebis denticulata* (Brongniart) Fontaine. MNCNV-7996. Imcomplete pinna of penultimate order. Bar: 5 mm.

Fig. 3.- *Cladophlebis denticulata* (Brongniart) Fontaine. MNCNV-7996. Pinna incompleta de penúltimo orden. Escala: 5 mm.

Fig. 4.- *Cladophlebis denticulata* (Brongniart) Fontaine. MNCNV-7993. Note rounded marks probably corresponding to sori (arrow). Bar: 5 mm.

Fig. 4.- *Cladophlebis denticulata* (Brongniart) Fontaine. MNCNV-7993. Observar las marcas redondeadas que probablemente corresponden a soros (Flecha). Escala: 5 mm.

Fig. 5.- *Otozamites mundae* (Morris) Teixeira emend. Pais. MNC-NV- 7999. Almost complete pinnate leave. Bar: 5 mm.

Fig. 5.- *Otozamites mundae* (Morris) Teixeira emend. Pais.. MNCNV- 7999 Fragmento de hoja pinnada casi completa. Escala: 5 mm.

Description. The material from Villela assigned to this species includes pinnate leaf fragments of terminal segments, preserved as calcite-filled impressions (part and counterpart).

Leaf once pinnate, leaflets attached to the adaxial surface of the rachis at 56º-60º, alternate, straight to slightly falcate, 8-13 mm long and 2 mm wide, regularly spaced, interspaces 0.5 mm, rounded apex and expanded basal angle on the acroscopic side of the leaflet that forms an auricle, poorly developed or not discernible. Leaflets flat, thick, with straight margins. Parallel venation can be observed in zones lacking infill.

Remarks. Although several specimens from Portugal have been described as: *O. ribeiroanus* (Heer, 1881, p. 9, pl. IX, fig.1-9), *O. angustifolius* (Heer, 1881, p. 9-10, pl. IX, fig. 10-13), and *O. natividade* (Teixeira, 1972, p. 121, pl. I-II), their morphological features indicate they are attributable to *O. mundae*.

In a study of *O. mundae* based on morphological and epidermal characteristics, Pais (1974) highlighted the close similarity between this species and those described by Heer and Teixeira. Thus, *O. ribeiroanus*, *O. angustifolius* and *O. natividade* should be regarded as synonyms.

Otozamites mundae also strongly resembles *O. gramineus* (Phillips) 1829 emend Harris 1969 in terms of the shape and size of its leaflets, despite a greater density of veins (Morris, 1849) and different cuticular features (Pais, 1974). These diagnostic features could not be observed in the specimens from Villela because of their state of preservation. However, despite corresponding in shape and leaflet arrangement to *O. gramineus*, the recovered specimens were assigned to *O. mundae* based on morphological differences such as: a smaller acroscopic basal margin (auricle) and leaflets on distal portions of leaves arising at a wider angle (60º-70º) than in *O. gramineus*.

Otozamites sp.

Material. MNCNV-7931, MNCNV-7945

Description. Portions of distal pinnate leaf zones with thick subopposite leaflets attached to upper surface of rachis, arising at 54º-56º. Leaflet bases slightly asymmetrical, acroscopic basal margin more developed than basiscopic, but lacking auricle. Veins parallel in central region of leaflets.

Remarks. Only two specimens of this taxon were observed at Villela. Both had similar features indicative of *Otozamites* but their fragmented nature and poor condition precludes their adscription to a given species of this genus.

Genus *Ptilophyllum* Brongniart 1828

Ptilophyllum pecten (Phillips) emend. Harris, 1969

Figure 6

Material. MNCNV-7939, MNCNV-7953, MNCNV-7969.

Description. Fragments of pinnate leaves, two corresponding to distal regions and one to the central leaf area. All present thick lanceolate leaflets, subalternate, parallel sided, apex obtuse and base asymmetric. Basiscopic margin decurrent and acroscopic margin rounded. Leaflets attached to the upper surface of the rachis, inserted at 54º- 58º-62º. The insertion angle depends on the location of the leaflets in the leaves, gradually narrowing towards the distal portion of the leaves.

Leaflets in the distal area 10.58-13.31mm long and 2.11-2. 67 mm wide. Subdistal area leaflets of identical morphology but slightly larger: 13.71 mm long and 2.7 mm wide. Irrespective of their position, leaflets are inserted at intervals of 0.5mm.

Remarks. The specimens from Villela well fit the diagnosis given by Harris (1969, p. 64-67) for the species. The leaflets are larger, but the width:length ratios were close to 1/5, which is characteristic of *P. pecten*.

Specimens referred to this species have been recorded from many Jurassic strata of both hemispheres (Seward, 1917: 524 et seq.) but not from latest Jurassic deposits hitherto.

Ptilophyllum pectiniformis (Sternberg) emend. Cleal and Rees, 2003

Figure 7

Material. MNCNV-7936, MNCNV-7938, MNCNV-7943, MNCNV-7947, MNCNV-7948, MNCNV-7952, MNCNV-7957, MNCNV-7958, MNCNV-7965, MNCNV-7968, MNCNV-7975, MNCNV-7998, MNCNV-8000.

Description. Portions of pinnate leaves with straight to falcate leaflets, apex acute and base asymmetrical, departing from the upper surface of the rachis at 60º-67º, inserted at intervals equal to less than 0.5 mm, and variable in size depending on their location on the leaf. Most apical leaflets are 10. 41-15. 63 mm in length, with leaflets inserted in the central leaf area, 17.03- 25.16 mm long. Width ranges from 1.73 to 3.6 mm, exceptionally reaching 4.1 mm. Leaflets show an acroscopic basal margin, rounded, not expanded, basiscopic decurrent, and thick to very thick lamina. Venation only appreciable in subapical region of leaflets where it is parallel.

Remarks. The specimens recovered closely resemble *P. pectinoides* (Phillips) Morris and their general morphological features coincide with those given for *P. pectinoides* (Harris, 1969, p. 57) for specimens from the Yorkshire Jurassic, except for the larger size of the bases. Despite these similarities, we ascribed the material to *P. pectiniformis* following the proposal of Cleal and Rees (2003, p. 756) of attributing remains of *P. pectinoides*-like leaves without cuticle to this species.

Fig. 6.- *Ptilophyllum pecten* (Pillips) emend. Harris. MNCNV-7939. Central part of a leaf with regularly spaced leaflets. Bar: 5 mm.

Fig. 6.- *Ptilophyllum pecten* (Pillips) emend. Harris. MNCNV-7939. Parte media de una hoja con foliolos regularmente espaciados. Escala: 5 mm.

Fig. 7.- *Ptilophyllum pectiniformis* (Sternberg) emend. Cleal and Rees. MNCNV- 7938. The most complete of collected specimens. Bar: 5 mm.

Fig. 7.- *Ptilophyllum pectiniformis* (Sternberg) emend. Cleal and Rees. MNCNV- 7938. El ejemplar mas completo de los colectados. Escala: 5 mm.

The fragments attributed to this species numerically dominate the flora of Villela, representing about 18% of the recovered remains. Most are highly fragmented: 2 cm – 4.5 cm; exceptionally they reach 6 cm. Most are preserved as densely encrusted, with limestone impressions of leaves lacking distal and basal portions.

Ptilophyllum sp. cf. *pectiniformes* (Braun) emend. Cleal and Rees, 2003

Material. MNCNV-7970.

Description.

Pinnate leaf incomplete, available length 29.25 mm. Leaflets lanceolate, subopposite, with thick lamina, emerging at an angle of 65º to the upper surface of the rachis, regularly spaced at intervals of 0.23 mm. Asymmetrical base, acroscopic basal margin slightly rounded, basiscopic basal margin decurrent. Venation non visible because of the infill and dense encrusting of the specimen.

Remarks. Only one specimen available as an imprint of the medial part of a leaf with 9 incomplete leaflets attached. Most showed their base and one half of their total length, lacking apex. The most complete leaflet lacks apex. It is 16.95 mm long and 3.73 wide. The shape and approximate size of the remaining leaflets could be inferred because of the good state of preservation of the existing leaflet.

The specimen broadly corresponds to *Ptilophyllum pectiniformis* in gross morphology, but the lack of apex and cuticle information precludes its assignment to this species.

Ptilophyllum acutifolium Morris, 1840

Figure 8

Material. MNCNV-7946.

Description. This is a single specimen of a pinnate leaf preserved as an impression (part and counterpart) in which apex and base are absent. The part is 44.48 mm long and the counterpart 63.0 mm long, total leaf width is 43.32 mm. Adaxially attached to the rachis, 11 complete and 2 incomplete leaflets can be observed. On average these are 23.20 mm long and 2.02 mm wide, subalternate, departing from the rachis at 70º, regularly spaced at 1 mm distances, with near-parallel sides and slightly falcate, gradually tapering to a very sharp apex giving the leaflets a mucronate appearance. Symmetrical base, rounded to truncate, without auricles, lightly constricted acroscopically and slightly decurrent basiscopically.

Remarks. The specimen collected at Villela is comparable to the material from India figured by Bose and Kasat (1972) on which Morris (1840) had based *P. acutifolium*. Although the specimen here described is broken at the level of the rachis, diagnostic characteristics, such as compact leaflet arrangement, insertion angle, slightly falcate acute apex and length:width ratio, are similar.

Dimensions of leaflets are slightly smaller than those given for this species including *P. acutifolium* var. *minor* stated by Wieland (1914) for material from the Liassic strata of Mixteca Alta (Mexico).

Fig. 8.- *Ptilophyllum acutifolium* Morris. MNCNV-7946. Leaf fragment showing falcate leaflets. Bar: 5 mm.

Fig. 8.- *Ptilophyllum acutifolium* Morris. MNCNV-7946. Fragmento de hoja con foliolos falcados. Escala: 5 mm.

Fig. 9.- *Ptilophyllum* sp1. MNCNV-7955. Detail of the central part of a leaf showing the bases of leaflets. Bar: 5 mm.

Fig. 9.- *Ptilophyllum* sp1. MNCNV-7955. Detalle de la parte central de una hoja mostrando la base de los foliolos. Escala: 5 mm.

Ptilophyllum sp.

Figure 9

Material. MNCNV-7955, MNCNV-7956

Description. Portions of pinnate leaves almost complete bearing subopposite to alternate leaflets, attached at 70º-75º to the upper surface of a rachis touching at their bases. Base parallel-sided on acroscopic margin, decurrent on basiscopic. Leaflets parallel-sided for most of their length, narrowing distally to rounded apex. No venation observable.

Remarks. The figured specimen (MNCNV-7955) consists of an impression (part and counterpart) of an almost complete pinnate leaf lacking the apex, but part of the petiole is preserved. Leaflets attached to the upper surface of the rachis, 14.5 mm long and up to 3.85 mm wide. The second unfigured specimen (MNCNV-7956) is similar except for the lack of the basal part and the size of the leaflets, which are 22.05 mm long and 3.58 mm wide.

Both specimens are similar in some features to *P. pecten* but differ from this species in the arrangement of the leaflets: the leaflets of *P. pecten* are regularly spaced whilst in the described specimens leaflets touch at their bases.

The lack of information on both cuticle and venation precludes the adscription of this material to a given species.

Genus *Pterophyllum* Brongniart 1828

Pterophyllum cycadites Harris and Rest 1966

Figure 10

Material. MNCNV-7935

Description. Fragment 7.34 cm long of a pinnate leaf with rachis 4.11 mm wide, slightly carenate with wide transverse protuberances (0.37 mm of width), in which opposite leaflets of round section, parallel margins and base slightly expanded are adaxially inserted at an angle of 85º-90º. Complete leaflets 21 mm long and 1.4 mm wide. Venation is not observed.

Remarks. Only one specimen was collected (MNCNV - 7935) from Villela that can be attributed with certainty to this species. It consists of an impression of the lower surface of the central part of a leaf that was partially broken on one side of the rachis. This specimen bears a dense travertine crust that, at several points, hindered the attachment of leaflets to the rachis. 29 leaflets preserved on one side of the rachis and 5 on the other. In addition, very fragmentary remains of leaflets exist with morphological features resembling those of *P. cycadites*.

This species was based on the Jurassic specimens from Yorkshire and up until now its palaeogeographical distribution was restricted to outcrops of that area.

Fig. 10.- *Pterophyllum cycadites* Harris and Rest. MNCNV-7935. Pinnate leaf fragment showing parallel-sided leaflets. Bar: 5 mm.

Fig. 10.- *Pterophyllum cycadites* Harris and Rest. MNCNV-7935. Fragmento de hoja pinnada con foliolos de márgenes paralelos. Escala: 5 mm.

Pterophyllum sp. cf. *thomasi* Harris 1952

Material. Two specimens: MNCNV-7929; MNCNV-7942

Description. Pinnate leaves bearing leaflets, adaxially inserted, departing from the rachis at an angle of 78º-80º, regularly spaced 1.15 mm, straight or slightly falcate near the subacute apex; 13.05 to 13.64 mm in length and 2.8 mm in width. Leaflet width remains constant along the leaflet, except for the apical area where it narrows abruptly.

Remarks. The morphology of the two specimens compares well with the material figured by Harris (1969, fig. 43 C) corresponding to distal parts of leaves attributed to *Pterophyllum thomasi*. Similarly, leaflet dimensions and other diagnostic characters, e.g. insertion angle, are almost exactly the same in both materials. However, rachis width is smaller in the specimens from Villela (7.7 mm). This suggests the Villela remains attributing to *P. tho-*

masi. Nevertheless, as indicated by Harris (1969, p. 96), the morphology of *P. thomasi* is similar in some repects to that of *P. jaegeri*, *P. subaequale* and *P. polonicum*, specimens of which are abundant from the Late Triassic to Lower Cretaceous. As in most cases of bennettitalean species, these only can be accurately identified through cuticle studies. Since the material examined is preserved as impressions, no cuticle analyses were possible and despite morphological similarities, we prefer to use open nomenclature to refer to these remains.

Zamites pumilio Saporta *emend.* Barale 1978
Figure 11
Material. MNCNV-7988; MNCNV-7989

Description. Distal portions of pinnate leaves with small-sized leaflets alternately arranged, inserted in the upper surface of the rachis, departing at 46º. Leaflets 6.4-6.9 long and 1.62-2.08 wide, base symmetrical.

Remarks. This species is rare at Villela, only two specimens having been collected.

Geographical and stratigraphical distributions of this species are restricted to the Kimmeridgian of Cerin, Corbonod and Lochien (France) (Barale, 1981).

Fig. 11.- *Zamites pumilio* Saporta *emend*. Barale. MNCNV-7988. Distal part of a leaf . Note symmetrical leaflet bases. Bar: 5 mm.

Fig. 11.- *Zamites pumilio* Saporta *emend*. Barale. MNCNV-7988. Parte distal de una hoja mostrando las bases simetricas de los foliolos. Escala: 5 mm.

Genus *Pseudocycas* Nathorst 1907
cf. *Pseudocycas* sp.
Figure 12
Material. MNCNV-7976

Description. Fragment of pinnate leaf with parallel-sided leaflets of rounded section and thick lamina inserted at 70º.

Remarks. The specimen recovered is 12.91 mm long and consists of a fragment of rachis with incomplete leaflets attached. Most complete leaflet 3 mm long, 2.2 mm wide. The whole width of the rachis cannot be observed because of breakage, neither can its characteristics given thast it is encrusted with recrystallized calcite.

The genus *Pseudocycas* was erected based on Cenomanian material (Nathorst, 1907).

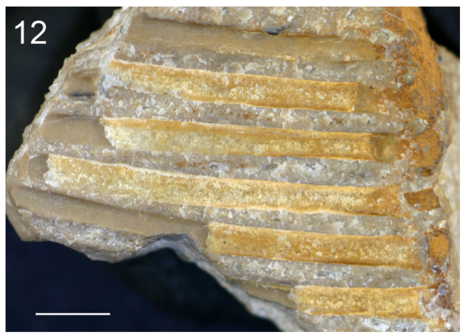

Fig. 12.- Bennettitales sp. cf. *Pseodocycas*. MNCNV- 7976. Thick leaflets of rounded section attached to a rachis. Bar: 5 mm.

Fig. 12.- Bennettitales sp. cf. *Pseodocycas*. MNCNV- 7976. Foliolos gruesos de seccion redonda unidos a un raquis. Escala: 5 mm.

5. Discussion and conclusions

The flora of Villela, composed of 8.2% fern and 71.8% Bennettitales-like foliage, seems impoverished compared to other macrofloras of roughly similar age described for the South European floristic province. The absence of common groups observed in the other macrofloras (e.g. conifers) could be the result of taphonomic processes. This is, however, unlikely since a number of these missing groups have a high preservation potential owing to characteristics such as the well-developed secondary wood and resistant cuticles of conifers. Another distinguishing feature of our finding is the sedimentary environment: a thermal hot-spring deposit related to an active fault occurring at the border of a major wetland system. Previously described floras have appeared in a coastal or marine sedimentary environment.

The exclusive fern-bennettitalean composition of the flora described here indicates a low diversity. However, considering the number of Bennettitalean taxa observed, this floristic group shows the highest diversity relative to other latest Jurassic-earliest Cretaceous floras, and could be ascribed to more extreme environmental and climatic conditions.

The global scarcity of Late Jurassic macrofloras is widely accepted (Vakhrameev, 1991; Cleal *et al.*, 2001). In addition, no accurate stratigraphical correlations exist between the well-known floras of southern England and southern Europe. Both globally and in the South European Floristic Province, the composition and distribution of these floras suggests a dry, sunny, subtropical type climate in which communities of Filicales, Pteridospermales, Cycadales, Bennettitales and conifers developed. The latest Jurassic-earliest Cretaceous vegetation of lower to mid-palaeolatitudes was characterized by strongly xeromorphic features, suggesting a dry-climate, partly-forested vegetation. These floras were of low diversity and dominated by microphyllous elements (conifers and cycadophytes).

Extant representatives of the Order Filicales show a wide geographical distribution and many have xeromorphic characters regardless of their place of growth. The species *Cladophlebis denticulata*, the only representative of this order in the flora examined here, is a common element of many Late Jurassic –Early Cretaceous floras, and does not, therefore, contribute to palaeoenvironmental and climatic models. In contrast, the numerically dominant Bennettitales group showing the greatest diversity in the flora examined here could be useful for reconstructing environmental and climatic conditions, since this group has been traditionally considered comprised xeromorphic plants. Characters such as pachycaulic stems, inflorescences of great size, intensely cutinized epidermis, sunken stomata with papillae, multicellular trichomes and cellular bodies that resemble the salt glands of some current plants (Sincock and Watson, 1988) corroborate the xerophytic nature of these plants. Additionally, Krassilov (1975) considered most Bennettitales to be anthracophiles, clarifying (*op. cit*., p.111) that this term is not equivalent to mesophyte or xerophyte but is useful for the reconstruction of adaptations to a moist regime. We consider that the presence of a single anthracophobic genus would be of little use in palaeoenvironmental reconstructions since some genera (e.g. *Ptilophyllum*) consist of both anthracophilic and anthracophobic species. Nevertheless, the presence of several anthracophobic Bennettitalean genera (*Ptilophyllum, Pterophyllum, Zamites and Pseudocycas*) and the absence of anthracophilic Cycadalean genera (*Nilssonia, Ctenis* and *Anomozamites*), along with additional characteristics (e.g. small leaves and thick leaflets) suggests that the Villela flora suffered arid conditions.

This conclusion is supported by global palaeontological and sedimentological data indicating that, since the beginning of the Late Jurassic, there was a widespread climatic trend across much of Europe towards more arid conditions, with a final arid stage in southern Eurasia during the latest Jurassic-earliest Cretaceous (Hallam, 1984; 1985; 1993; Vakhrameev, 1991; Ziegler *et al.*, 1993).

In a more restricted context, and based on sedimentological data, a semi-arid Mediterranean-type climate for the western Iberian Peninsula was proposed previously by Wright and Wilson (1987) (*fide* Valdés and Sellwood, 1992). Hernández (2000) confirmed this palaeoclimatic model for the Aguilar Basin during the Berrisian based on sedimentological evidence in the Aguilar Formation, such as humectation-desiccation carbonate sequences (similar to the sequences in the Everglades of Florida), laminar calcretes and evaporite levels (dolomite and gypsum pseudomorphs).

Based on the available sedimentological and palaeobotanical data, we infer that the xerophytic macroflora of Villela was well suited to a dry-savannah i. e. wide open, partially forested areas, with a predominance of small or medium-sized habit, drought resistant elements (Bennettitales). In effect, Batten (1975) first proposed Bennettitales as the low-standing elements of a dry-savannah and later on, Rees *et al.* (2004), using data from climate-sensitive sediments, fossil plants and dinosaurs, also inferred a savannah-like landscape for the Tendaguru and Morrison formations of East Africa and North America, respectively.

The Villela flora has several taphonomic implications. Imprints of plant specimens are arranged parallel and perpendicular to the bedding plane, in a three-dimensional orientation that suggests reworking. Additionally, the plant remains are coated with a microbial film up to 5 mm thick that may be easily distinguished from the travertine rock matrix (Hernandez *et al.*, 1998) (Fig. 13). This biofilm is made up of: 1) cyanobacterial filamentous and brush-like growth structures; 2) laminated cyanobacterial mats; 3) simply deposited bacterial clumps; 4) wavy bacterial lamination; 5) bacterial filaments; and 6) undetermined filaments.

Bacterial microfabric is the most abundant component of the biofilm and is characterized by filamentous and shrub-like colonies. The cyanobacterial microfabric shows two different morphologies: fan-shaped forms (like those produced by the actions of Rivulariaceae and

Fig. 13. - Interpretative drawing of a tranverse section through an specimen. b1) bacterial clumps; b2) bacterial lamination, b3) bacterial filaments; c1) brush-like cyanobacterial colonies; c2) Cyanobacterial filamentous structures; m) macrophyte remain.

Fig. 13. – Dibujo a cámara clara de la sección transversal de un ejemplar. b1) acumulación de bacterias aisladas; b2) laminación bacteriana; b3) filamentos bacterianos; c1) colonias arborescentes de cianobacterias; c2) mallas finamente laminadas de cianobacterias; m) macrorresto.

Ortonella); and finely laminated shapes (probably due to *Girvanella*).

The macroflora here described, besides being the first record of *Ptilophyllum pecten* from Tithonian-Berriasian sediments, broadens the geographical and stratigraphical range of *Pterophyllum cycadites* and *Zamites pumilio*.

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